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Lateral interactions in amblyopia

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Abstract

We studied lateral neural interactions in strabismic ($n = 6$) and anisometropic amblyopes ($n = 3$) by measuring reductions in the perceived contrast of a foveally viewed Gabor centred in a horizontal array of closely neighboring Gabors. Strabismic amblyopes, but not anisometropic amblyopes, failed to show the reduction in perceived contrast typical of normal vision [J. Opt. Soc. Amer. A 15 (1998) 1733] when lateral contrast information is available at the same orientation and spatial frequency. The strabismic amblyopes also severely misperceive the regularity of the array of Gabors flanking the test stimulus. A normal eye could model the anomalous contrast perception of the amblyopic eye, by adding an equivalent amount of spatial distortion to the stimulus. The relationship between the observed anomalies for local contrast gain control and positional sensitivity is discussed.

Keywords: Amblyopia; Strabismus; Anisometropia; Spatial interactions; Apparent contrast

1. Introduction

Amblyopia is a common developmental visual disorder in which visual processing through the amblyopic eye is anomalous. Two principal causes of amblyopia are strabismus (misaligned eyes during development) and anisometropia (unequal refraction between the eyes during development). The site of the anomalous processing in amblyopes is the visual cortex (Cleland, Crewther, Crewther, & Mitchell, 1982; Hess & Baker, 1984) but its exact nature is still unclear. Though it is well documented that Amblyopes experience reductions in contrast sensitivity (Hess & Howell, 1977; Levi & Harwerth, 1977), this is not their sole, or even, their main problem (Hess & Holliday, 1992; Levi & Klein, 1983). Amblyopes also perceive spatial distortions in images (Bedell & Flom, 1981; Fronius & Sireteanu, 1989; Hess, Campbell, & Greenhalgh, 1978; Lagreze & Sireteanu, 1991; Sireteanu, Lagreze, & Constantinescu, 1993) and have deficits in localizing the position of closely spaced (Levi & Klein, 1982) and widely spaced (Hess & Holliday, 1992) image features.

There appear to be clear differences in the pattern of visual deficits between strabismic and anisometropic amblyopes that provide insight into the nature of the mechanisms of amblyopia (Hess & Bradley, 1980; Hess, Campbell, & Zimmern, 1980; Hess & Holliday, 1992; Hess & Pointer, 1985; Sireteanu et al., 1993). In strabismic amblyopia the deficits in positional localization and in contrast sensitivity appear unrelated whereas in anisometropia the deficits in positional localization are less severe and follow as a consequence of the deficits in contrast sensitivity (Hess & Holliday, 1992). Two main types of explanations are advanced to account for the anomalous vision of strabismic amblyopia. One explanation suggests a passive mechanism that involves a degraded spatial representation caused either by a reduction in the number of neurons (Levi & Klein, 1986) or by disarray in the spatial relationships of neurons (Hess & Field, 1994). A second explanation suggests an active mechanism involving anomalous interactions between neural networks designed to accomplish specific roles in vision (Lowel & Singer, 1992; Polat, Sagi, & Norcia, 1997; Roelfsema, Koenig, Engel, Sireteanu, & Singer, 1994). This latter suggestion originally came from the clinical observation that amblyopes experienced more profound lateral interactions from adjacent contours, a phenomenon known as "crowding", and from the finding that discriminative functions were

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selectively anomalous in amblyopia (Hess, Burr, & Campbell, 1980). More recently, Polat et al. (1997) used a contrast detection task in which lateral flanking contours of a specific orientation facilitate detection in normal vision, to argue that lateral interactions are anomalous in amblyopia and that the form of this anomaly varies greatly among different amblyopes.

We do not as yet have a clear idea which visual tasks critically rely on lateral interactions and which do not. Monocular tasks that have been identified as requiring a network as opposed to a single cell explanation include contour integration (Field, Hayes, & Hess, 1993), motion trajectory detection (Verghese, Watamaniuk, McKee, & Grzywacz, 1999) and contrast discrimination (Wilkinson, Wilson, & Ellemberg, 1997). Recently, Ellemberg, Wilkinsion, Wilson, and Arsenault (1998) have shown that the perceived contrast of an isolated Gabor patch in a string of Gabors depends on the spacing, orientation and spatial frequency of neighboring Gabor patches. This finding suggests that perceived contrast in any localized region is a function of the neural activity coming from adjacent regions; a clear case requiring a network rather than a single cell explanation (Cannon & Fullencamp, 1991; Ellemberg et al., 1998).

In the light of the above anomalous lateral interaction hypothesis for amblyopia, we wondered whether the perceived contrast of an isolated Gabor patch is correctly perceived by the amblyopic visual system. Using a similar paradigm to that of Ellemberg et al. (1998), we measured the apparent contrast of a Gabor centered in a horizontal array of Gabors. We also measured the detection of spatial misalignment within the string of micropatterns. Participants were six strabismic amblyopes and three anisometropic amblyopes. The results indicate that strabismic amblyopes, but not anisometropic amblyopes, fail to show the reduction in perceived contrast typical of normal vision when lateral contrast information is available at the same orientation and spatial frequency.

2. Methods

2.1. Subjects

Participants were six adults with infantile strabismic amblyopia and three adults with infantile anisometropic amblyopia. They underwent standard orthoptic testing in which their strabismus was measured using a cover test (for distance viewing), the normality of their fundus was verified by ophthalmoscopic examination, the degree of eccentric fixation was measured using visuoscopy and their refraction checked using subjective means. They were all adults in the age range 22–57 years with normal ocular media. None of the subjects suffered from any other visual pathology. An interocular refractive difference exceeding 2 dioptres in spherical or cylindrical

Table 1

Subject	Amblyopic eye/ type	Age (year) at first patching/surgery	Acuity	Correction	Fixation N = nasal; I = inferior; S = superior	Strabismus et = esotropia; xt = exotropia
CT	LE/strab	6/none	6/6 6/60	PL PL + 3.25 × 90	Central 3.0S	5° LET
CP	RE/strabaniso	5/none	6/18 6/6	−5.25 − 2.25 × 180 −3.0 − 1.75 × 170	2.0T Central	Intermittent 5° RXT
VE	LE/strab	None/none	6/6 + 2 6/24	+1.75 +2.0	Central Central	6° LXT
JF	LE/strabansio	None/none	6/4 − 5 6/72	−2.25/ − 1.5 × 5 −3.00/ − 4.25 × 180	Central 3.0 N	5° LET
OA	RE/strabaniso	Not available	6/24 6/9	+4.50 − 5.00 × 30 −1.75 − 1.75 × 150	4.0 NS Central	5° RET
PY	RE/strabaniso	5/patching	2/60 6/6	−8.50/ − 1.00 × 120 −4.00/ − 1.00 × 165	3.0 Nasal	10° RXT
J.G.	RE/aniso	4/patching	6/60 6/5	+5.00 + 1.25 × 100 +2.00	Central	None
M.P.	LE/aniso	8/no patching	6/5 6/18	PL +3.00/ − 1.50 × 50	Central	None
V.S.	LE/aniso	8/patching	6/5 6/9	−1.25 +4.00 − 2.00 × 70	Central	None

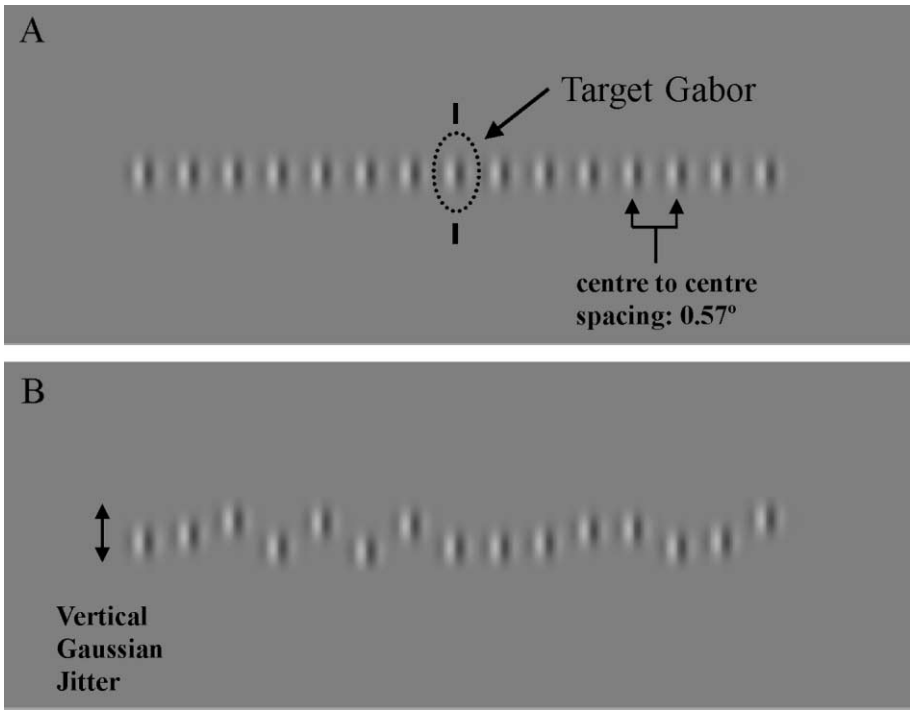

Fig. 1. (A) Example of the stimulus configuration for the apparent contrast task. The array consisted of equally spaced vertically oriented Gabors aligned along the horizontal axis. Vertical and horizontal space constant were 0.19°, spatial frequency was 3.3 c deg^{-1}, and contrast was 40%. The target Gabor was always the one at the centre of the array and was always presented at fixation. In the schematic its position is delimited by the dashed ellipse; however, during the experimental procedure its position was indicated only by the two vertical markers, one above and below the central Gabor. (B) Example of the stimulus configuration for the jitter detection task. The parameters of the Gabors and of the stimulus configuration are the same as indicated above, except that each Gabor is jittered on the vertical axis according to a Gaussian function.

power was classified as anisometropic. All were experienced psychophysical observers and none was aware of the issues being investigated. Clinical details for each subject are presented in Table 1.

2.2. Stimuli

The stimuli were a horizontal one-dimensional array of vertically oriented, spatially localized two-dimensional Gabors. The array contained 15 equally spaced Gabor micropatterns (see Fig. 1). The string of micropatterns had a horizontal extent of 10.8° and a centre to centre inter-element spacing of 0.57° (1.8 cycles of the Gabor carrier, where each cycle is 18.2′).

Gabor elements are sine-wave gratings multiplied by a Gaussian in the horizontal (σ_x) and orthogonal (σ_y) dimensions. This is given by the following equation:

$$G(x,y) = L[1 + C\exp(-x^2/\sigma_x^2)X\exp(-y^2/\sigma_y^2)\sin(2\pi\sigma x)], \quad (1)$$

where L is the mean luminance of the pattern, σ is the spatial frequency of the sine-wave, C is the contrast of the stimulus, and (σ_x) and (σ_y) are respectively the horizontal and vertical space constants (the distance from the element's centre at which its amplitude envelope decreases to $1/e$). In the present study each Gabor had a vertical and horizontal space constant (σ_y and σ_x, respectively) of 0.19°, a contrast (C) of 40%, and a vertical carrier frequency (σ) of 3.3 c deg^{-1}. These parameters were chosen so that the stimuli would be highly visible to the amblyopic eyes.

The stimuli were generated on a Macintosh G3 computer and were displayed on a monitor with a frame rate of 75 Hz and a pixel resolution of 832 × 624. The stimuli were produced by means of a linearized subset of gray values. Mean screen luminance was maintained at 20 cd m^{-2}.

2.3. Procedure

In a dimly illuminated room, observers viewed the screen from a distance of 33 cm. Subjects were tested monocularly, both with their amblyopic eye and with their non-amblyopic eye. At the beginning of each trial, subjects were instructed to fixate a small cross at the centre of the uniformly illuminated screen. In consecutive experiments, apparent contrast and jitter detection were measured using a two-alternative temporal forced choice paradigm and the method of constant stimuli. The stimuli were always presented foveally.

2.3.1. Apparent contrast

We measured the apparent contrast of the central Gabor patch embedded in an array of similar patches using a contrast matching paradigm (see Fig. 1A). The position of the target Gabor in the array, the one upon which the contrast judgement was to be made, was indicated by markers. That is one thin dark stripe above and one below the central Gabor. The contrast of the central target Gabor in the array was compared to that of a single Gabor patch appearing in the same spatial location but either before or after in time. The contrast of each Gabor micropattern in the array was set to 40%. The contrast of the single, isolated Gabor was presented at one of five contrast values so as to span the psychometric function. The array and single Gabor were presented in random order for a duration of 250 ms each, separated by a 500 ms interval during which the screen returned to the mean luminance. Each interval was marked by a tone. Subjects indicated by means of one of two key-presses which interval contained the Gabor with the highest contrast. For comparison, and to obtain a baseline we also measured the apparent contrast of an isolated Gabor patch.

2.3.2. Jitter detection

We measured the minimum amount of jitter in the vertical dimension necessary to detect spatial misalignment in a similar array of horizontally-aligned Gabor micropatterns (see Fig. 1B). One interval contained a baseline array, where each micropattern was centred on the same horizontal axis; the other interval contained a jittered array, where the individual Gabors were jittered vertically according to a Gaussian function. The jitter in the misaligned array was presented at one of five jitter values as to span the psychometric function. The baseline array and the jittered array were presented in random order for 250 ms each, separated by a 500 ms interval during which the screen returned to the mean luminance. Each interval was marked by a tone. Subjects indicated by means of one of two key-presses which interval contained the array with the vertical jitter or misalignment.

Three thresholds were measured for each of the three conditions (apparent contrast of the central Gabor in the array; apparent contrast of a single Gabor; and jitter detection). Each threshold was calculated from 125 trials (25 trials for each of five contrast or jitter test values). In addition, subjects had a practice run with each of the three conditions before moving on to the main experiment.

For apparent contrast, the psychometric functions were fitted to each data set with a cumulative normal fit, from which we estimated the 50% probability level, or point of perceptual equality. For jitter detection, the psychometric functions were fitted to each data set with Quick or Weibull functions, and the maximum-likelihood estimate of 75% correct.

3. Results

3.1. Apparent contrast

The effect of the flanking Gabors on the apparent contrast of the central Gabor micropattern is shown in Fig. 2 for each normal eye and amblyopic eye of strabismic amblyopes. These thresholds were derived from fitting the psychometric data with a cumulative normal function and deriving the contrast corresponding to 50% correct. The error bars represent ±1 standard error from repeated runs. The white bars present data for the condition where there was no flanking Gabors,

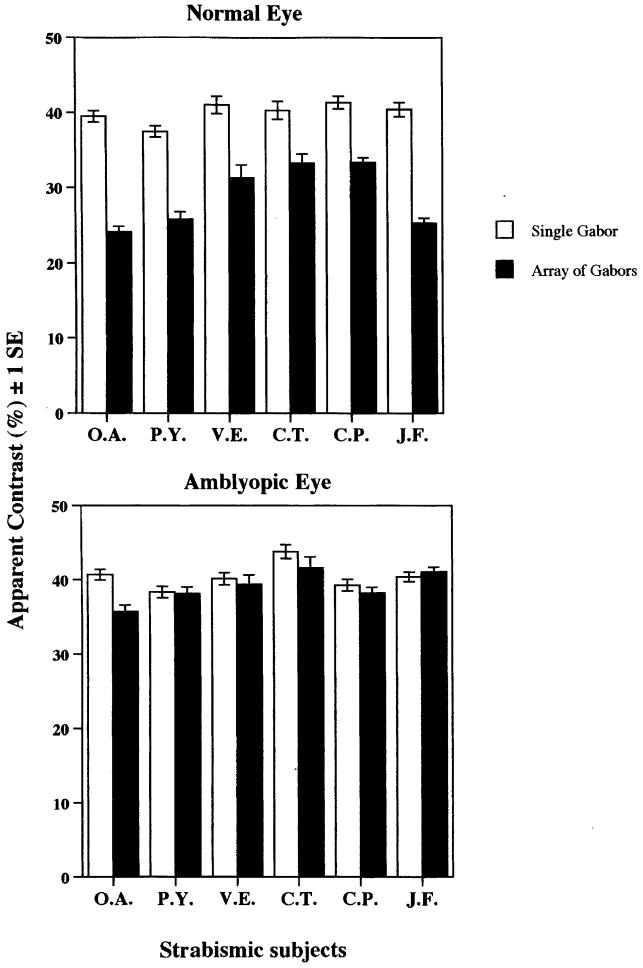

Fig. 2. Mean apparent-contrast for the normal and amblyopic eyes of each of six strabismic amblyopes. The white bars present data for the condition where there was no flanking Gabors and the black bars present the data for the condition where the target Gabor was embedded in the array of flanking Gabors. Error bars are ±1 SE.

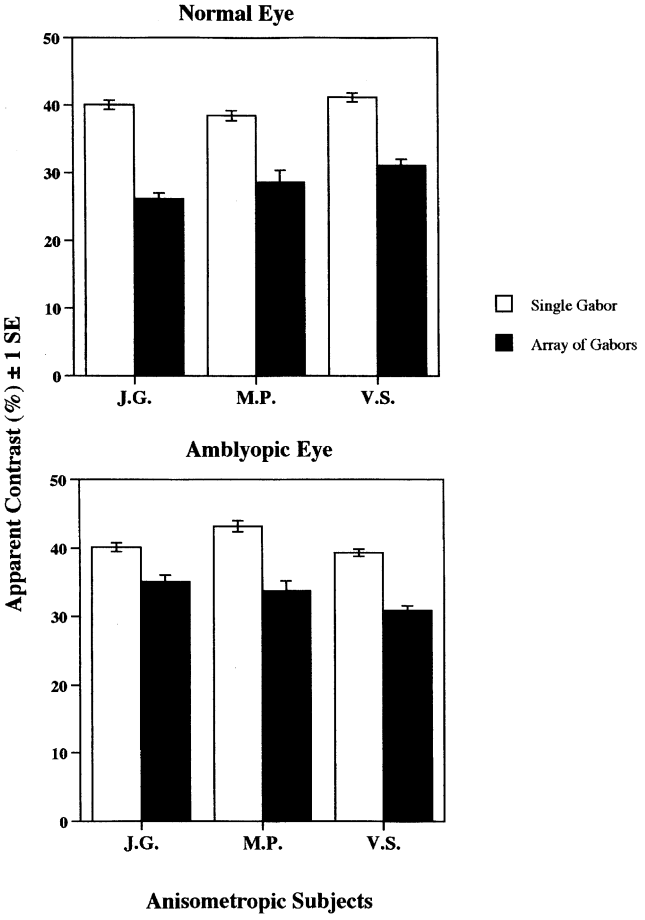

Fig. 3. Mean apparent-contrast for the normal and amblyopic eyes of each of three anisometropic amblyopes. The white bars present data for the condition where there was no flanking Gabors and the black bars present the data for the condition where the target Gabor was embedded in the array of flanking Gabors. Error bars are ±1 SE.

and the black bars present the data for the condition where the target Gabor was embedded in the array of flanking Gabors. As expected, the apparent contrast of an isolated Gabor patch matched its physical contrast, both for the normal and amblyopic eyes. Similar to what was reported by Ellemberg et al. (1998), normal eyes experienced a reduction in apparent contrast on average by 28% for the flanking condition. In contrast, unlike normal eyes, strabismic eyes experienced little if any reduction in the apparent contrast of the flanked Gabor micropattern (2.5% reduction).

The data for the same conditions are presented in Fig. 3 for each normal eye and amblyopic eye of anisometropic amblyopes. Like for strabismic subjects, the apparent contrast of a single Gabor patch matched its physical contrast, both for the normal and amblyopic eyes. Furthermore, normal eyes also experienced a reduction in the apparent contrast of the flanked Gabor that averaged 28%. However, unlike the strabismic amblyopes, the amblyopic eyes of the anisometropic amblyopes did perceive a reduction in the apparent contrast of the flanked Gabor pattern (mean reduction = 18%).

3.2. Jitter detection

Fig. 4 shows the minimum amount of jitter necessary for strabismic and anisometropic amblyopes, to detect misalignment in the array. The white bars show the data for normal eyes and the black bars for the amblyopic eyes. The minimum amount of jitter (expressed as the standard deviation of a Gaussian) necessary to detect misalignment averaged 0.06° in normal eyes. In contrast, strabismic eyes required 0.95° jitter to detect misalignment in the array. Anisometropic eyes were also worse than normal eyes, with an average of 0.30° jitter necessary to detect the misalignment. However, their performance was still better than that of strabismic eyes by a factor of 3.

3.3. Modeling the effects of spatial distortion of apparent contrast

The results from the experiment on jitter detection indicate that strabismic amblyopes perceive the array of Gabors as being greatly distorted in its spatial disposition. In fact, they perceive three times more spatial distortion in the array than do the anisometropic amblyopes. The strabismic eye requires that the individual elements contain about 0.95° jitter to detect any distortion in additional to their intrinsic baseline perception of distortion. To test whether there is any relationship between distortion in the stimulus array and anomalous visual response to spatial interactions, we measured the apparent contrast of an observer with normal vision for arrays that contained different amounts of vertical Gaussian jitter. In Fig. 5 we plot the amount of perceived contrast for the central Gabor in our array (relative to an isolated Gabor that is set to 40%) against the amount of vertical Gaussian jitter of the array. The results show that as vertical spatial alignment of the array is perturbed, the perceived contrast of the central Gabor becomes similar to that of the isolated Gabor (i.e., 40%), that is, there is reduced influence of the flanking Gabors. Specifically, as the vertical Gaussian jitter increases to 0.5°, the reduction in apparent contrast diminished by half. When the array contains 1.0° of vertical Gaussian jitter, the same amount of spatial distortion as that perceived by the strabismic amblyopes, the normal observer no longer experiences any reduction in the apparent contrast of the flanked Gabor. Therefore, there may be an association between the strabismic amblyopes' anomalous contrast perception of the target Gabor and the amount of spatial jitter or misalignment that they perceive/tolerate in the stimulus array.

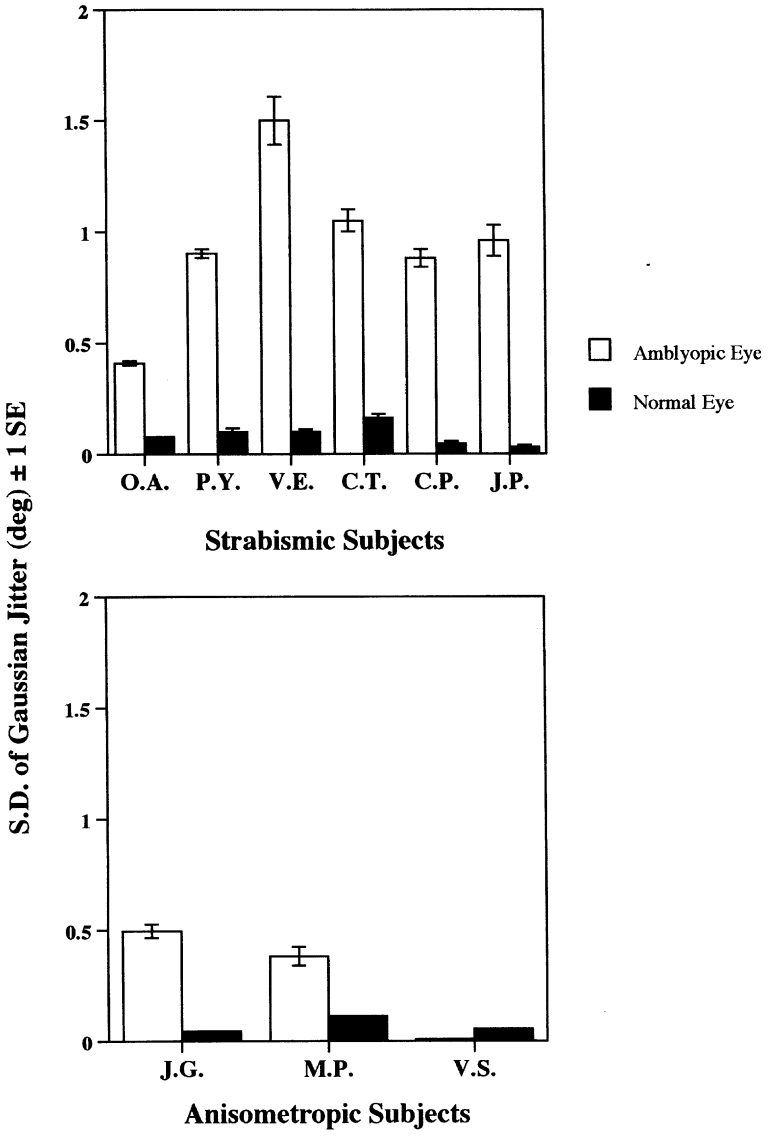

Fig. 4. Mean Gaussian jitter necessary to detect misalignment in the array for each amblyopic eye (white bars) and normal eye (black bars) of the six strabismic amblyopes (top panel) and of the three anisometropic amblyopes (bottom panel). Error bars are ±1 SE.

4. Discussion

We find that the amblyopic eye of subjects with developmental strabismus did not perceive any change in the contrast of the central Gabor target when flanked by closely neighboring Gabors. In contrast, all normal eyes as well as the amblyopic eye of patients with developmental anisometropia perceived a reduction in the apparent contrast of the central Gabor target. Using a one-dimensional textured surface made of Gabor micropatterns, like the one used in the present study, Ellemberg et al. (1998), found that the apparent contrast of a target Gabor was greatly reduced when flanked by closely neighboring Gabors of like orientation and spatial frequency. This reduction in apparent contrast disappeared as the distance between the Gabor elements increased and the perception of texture coherence broke down. Modeling efforts (Wilkinson & Wilson, 1999) suggest that at inter-element spacings that give rise to the perception of texture, like the spacing used in the present study, long-range spatial interactions between spatial filters (akin to simple cells) become activated and the threshold for spatial pooling by complex cells is met. As a consequence, information about individual texture components is lost and the perceived contrast of these individual components is reduced. This is an example of an important lateral interaction thought to occur between cells in the early part of the cortical pathway involving a contrast gain control (Heeger, 1992). Therefore, the findings from the present study indicate that

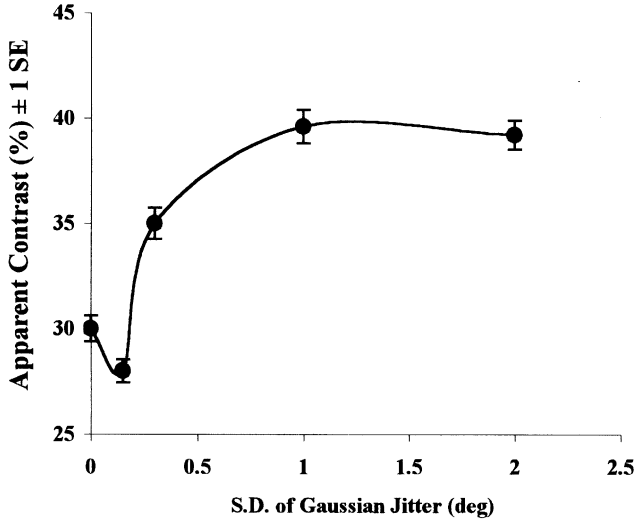

Fig. 5. Mean apparent contrast for an observer with normal vision tested with arrays that contained vertical Gaussian jitter. Error bars are ±1 SE.

early abnormal visual experience caused by developmental strabismus results in an abnormality involving spatial interactions subserving local contrast gain control.

In the strabismic subjects, we did not find a significant correlation between the deficits for acuity and contrast gain ($r = 0.267$; $p < 0.10$). This is not unexpected for a number of reasons. First, all stimulus parameters were well within the visual bandpass of the amblyopic eyes of each patient: the Gabors had a contrast of 40%, a peak spatial frequency of 3.3 c deg^{-1}, and a circular symmetric space constant of about 0.20°. Second, Hess and Bradley (1980) showed that strabismic amblyopes have normal contrast perception above threshold. Third, the subjects in the present study reported that the stimuli were equally visible to their normal and amblyopic eyes. Finally, several studies have made the case that the deficits of strabismic amblyopes in the spatial coding of visual information, such as spatial localization and contour integration, are unrelated to their losses in contrast sensitivity (Hess & Field, 1994; Hess & Holliday, 1992; Hess, McIlhagga, & Field, 1997).

Our findings are suggestive that early developmental strabismus and anisometropia have different effects on the later visual response of the amblyopic eyes to the spatial interactions subserving local contrast gain control. Strabismic eyes failed to perceive a reduction in apparent contrast that is normally caused by long-range interactions among the spatial filters within the gain pool that is activated by the row of adjacent Gabor micropatterns. On the other hand, albeit smaller than normal, anisometropic eyes perceived the expected reductions in the apparent contrast of the flanked Gabor. As noted earlier, it is well established that strabismic and anisometropic amblyopes also show deficits in contrast sensitivity and spatial localization or positional sensitivity (Bradley & Freeman, 1985; Fronius & Sireteanu, 1989; Hess & Holliday, 1992; Lagreze & Sireteanu, 1991; Levi & Klein, 1982; Sireteanu et al., 1993). However, there are clear differences in the pattern of visual deficits between strabismic and anisometropic amblyopes. First, the contrast deficit is distributed differently across the visual field in these two conditions (Hess, Campbell, & Zimmern, 1980; Hess & Pointer, 1985). Second, in strabismic amblyopes the spatial deficits do not co-vary with either contrast sensitivity (Hess & Holliday, 1992) or resolution (Levi & Klein, 1983), whilst in the majority of anisometropic amblyopes the deficits in spatial localization could be explained by the deficits in contrast sensitivity and resolution. Therefore, the amblyogenic factors in anisometropia versus strabismus appear to be carried, at least in part, by different mechanisms: in anisometropic amblyopes, the deficit in contrast sensitivity provides a more complete account of their losses, whilst in strabismic amblyopes, there are additional deficits in spatial coding that are unrelated to the losses in contrast sensitivity. Therefore, the fact that deficits are more severe in strabismic amblyopes (only two of the three anisometropic amblyopes are slightly worse than normal) provides further evidence that there may be different amblyogenic mechanisms in these two forms of amblyopia.

The present results suggest that visual performance on a task shown to depend on a particular type of lateral neural interaction in normal vision (Ellemberg et al., 1998), is abnormal in amblyopia, especially strabismic amblyopia. We also show that strabismic amblyopes severely misperceive the regularity of the array of Gabors flanking the test stimulus. Indeed, the degree of perceived irregularity by the amblyopic eye would be sufficient in itself to explain the anomaly in perceived contrast for this task. This offers a simple explanation for the fact that, in amblyopia, contrast of an isolated image feature is not as influenced by its surrounding features as one might expect from findings in normal vision (Ellemberg et al., 1998). If there is a positional abnormality in amblyopia that precedes or occurs at the same point as the contrast/gain computation that underlies this task, then such an abnormality in contrast-coding would be expected. Therefore, instead of postulating a primary abnormality in the nature of the lateral neural interactions subserving contrast gain control within a faithful topographical representation (Polat et al., 1997), a simpler explanation might be normal gain control but within a disturbed topographical representation. In this case the primary deficit would be the anomalous lateral interactions subserving positional coding of non-overlapping image features rather than anomalous lateral interactions subserving the contrast gain control mechanism per se. A similar conclusion was arrived at from a study of contour integration in strabismic amblyopia, where the degree of

perceived topographical disruption was shown to quantitatively account for the measured anomaly to contour integration (Hess et al., 1997). The results of Polat et al. (1997) are also potentially open to reinterpretation within such a framework. The other possibility is that the observed deficits to contrast gain control and positional coding are not causally related. They could be both caused by a single, common but as yet unidentified anomaly.

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